

Prey Fragmentation and Transport in Six Tropical Arboreal Ant Species

Tadu Zephirin^{1,*}, Messop-Youbi Edith Blandine^{1,2}, Fomekong Lontchi Judicael¹,
Alene Desiree Chantal¹, Djieto-Lordon Champlain¹

¹Department of Animal Biology and Physiology, Faculty of Science, University of Yaoundé 1, Yaoundé, Cameroon

²Department of Zoology and Animal Physiology, Faculty of Science, University of Buea, Buea, Cameroon

Email address:

zephirin_tadu@yahoo.ca (Tadu Z.), emessop@yahoo.fr (Messop-Youbi E. B.), judicaelfomekong@gmail.com (Fomekong L. J.),

chantalalene@yahoo.fr (Alene D. C.), champlain_djieto@yahoo.ca (Djiéto-Lordon C.)

*Corresponding author

To cite this article:

Tadu Zephirin, Messop-Youbi Edith Blandine, Fomekong Lontchi Judicael, Alene Desiree Chantal, Djieto-Lordon Champlain. Prey Fragmentation and Transport in Six Tropical Arboreal Ant Species. *Computational Biology and Bioinformatics*.

Vol. 9, No. 1, 2021, pp. 21-30. doi: 10.11648/j.cbb.20210901.13

Received: May 17, 2021; **Accepted:** June 3, 2021; **Published:** June 25, 2021

Abstract: Prey fragmentation and transport modalities were studied in *Myrmecaria opaciventris*, *Platythyrea conradti*, *Crematogaster* sp., *Crematogaster clariventris*, *Tetramorium aculeatum* and *Oecophylla longinoda*, six tropical ant species with varying levels of adaptation to foraging in the tree canopy. Termites and grasshoppers of different sizes were used as prey and deposited on a hunting arena. After prey capture, we investigated the strategy adopted by each ant species to fragment and transport their prey. The data were analyzed with classification tree, using Chi-squared Automatic Interaction Detection method to find the variation in prey fragmentation strategies and transportation modalities between arboreal ant species in relation with prey type and prey size. The results showed that prey fragmentation did not occur systematically after capture and varied between ant species with prey type and prey size. Studied ant species cut their prey either completely into tiny pieces or partially into two or three large pieces before cutting them totally into tiny pieces or not at all. Fragmentation strategy, induced variation in transport modalities including (a) transport of large pieces, each by a single worker; (b) transport of large pieces, each, by a group of workers; (c) transport of tiny pieces after total cutting, and (c) transport of entire prey in the nest without fragmentation. Prey fragmentation and transport modalities varied between ant species in relation with their level of adaptation to arboreal area.

Keywords: Ant, Prey Capture, Prey Fragmentation, Hunting

1. Introduction

In their environment, ants exploit diverse food items including prey, making them generalist predators, scavengers and omnivores [1]. Ants need to forage in their territory to find food. Foraging is thus the basis for the survival, development and reproduction of animals [2]. Prey capture involve the following behavioral acts: detection; attack and seizure; recruitment or not (depending of ant species); spread-eagling or not (depending of ant species and prey sizes), fragmentation (varies among ant species and prey sizes) and transport by a single worker or by several workers [1]. Recruitment of nestmates during prey capture appears to

be a crucial stage that determines the success of the prey capture in many arboreal ant species. Nestmates are recruited using various mechanisms including (1) stochastic individual strategies by a single worker, (2) stochastic collective or tandem strategies found in ponerine ants [3], (3) group recruitment strategies with limited or (4) unlimited group sizes found in various myrmicine and formicine species [4, 5], and (5) leader-independent trail communication found in the formicine genus *Polyrhachis* [5]. After recruitment, huntresses of many arboreal ants species, cooperatively spread-eagle the prey. This prey is subsequently cut up before being transported as seen with *Tetramorium aculeatum* Mayr [6] and *Crematogaster* sp. [7]. In some arboreal ant species like *Platythyrea conradti* Emery [8] and

Oecophylla longinoda Latreille [9], preys are transported to the nest without being cut up. Looking at the fragmentation approach adopted by many ant species, [10] found that workers of most arboreal ants cut-up large prey at the site retrieve them and bring smaller pieces to the nest while in most ground-living ant species, a group of workers retrieve large prey cooperatively without fragmentation with or without recruitment. From the above, we hypothesize that prey fragmentation and transport modalities varies in ant species with respect to their level of arboreal adaptation. To achieve this, we compared the fragmentation strategy during prey capture in six tropical ant species to find (1) the influence of prey type, prey size and morphological caste on the occurrence of prey fragmentation and (2) the influence of prey size on fragmentation strategy, and their implication in the transportation modalities.

2. Material and Method

2.1. Study Site

The study was conducted in the Minkoa Meyos orchard (02°31', 10°55') near Yaoundé, and in the zoology laboratory at the University of Yaoundé 1, in Cameroon. Yaoundé is characterized by a subequatorial climate with a bimodal rainfall regime. The four distinct seasons are: two wet and two dry seasons. Rainfall averages is about 1700 mm per year and the mean annual temperature is about 25°C. Minkoa Meyos orchard is an experimental station for fruits trees of "Institut de Recherche Agronomique pour le Développement (IRAD)". The orchard is comprised of *Mangifera indica*, *Dacryodes edulis*, *Psidium goyava*, *Carica papaya*, *Elaeis guineensis*, *Citrus sinensis*, *Citrus limon*, *Citrus medica*, planted in a regular spatial pattern. Plots of *Zea mays*, *Manihot esculenta*, *Xanthosoma* sp., *Musa sapienta* and *Musa paradisiaca* were intermingled haphazardly within the orchard.

2.2. Studied ant Species

The study was conducted on six ant species belonging to 3 sub-families (Formicinae, Myrmicinae, and Ponerinae) and 5 genera (Myrmecaria, Platythyrea, Crematogaster, Oecophylla and, Tetramorium). Ant species studied were selected according to their level of arboreal adaptation. We selected *Myrmecaria opaciventris* Emery, 1893 (Myrmicinae) a ground-dwelling ant species with arboreal habit [11], *Platythyrea conradti* Emery, 1899 (Ponerinae) a primitive arboreal ant species [8] and four ecologically dominant arboreal ant species found in great frequency of abundance and frequency of occurrence on the cocoa trees in agroforestry systems in south Cameroon [12, 13]: *Crematogaster* sp. (Myrmicinae) also call *Crematogaster* "tsapi" by [7], *Crematogaster clariventris* Mayr, 1895 (Myrmicinae), *Tetramorium aculeatum* Mayr, 1866 (Myrmicinae) and *Oecophylla longinoda* Latreille, 1802 (Formicinae).

2.3. Experimental Apparatus

2.3.1. Ground-dwelling ant Species with Arboreal Habit

Ground-dwelling ant species with arboreal habits are species that nest in the soil and forage in trees to collect floral and extrafloral nectars [11]. Experiments were conducted on 10 colonies of *M. opaciventris* within the Minkoa Meyos orchard. Two rectangular plywood sheets (40 x 40 cm) were placed on the soil at three meters from the principal tunnel. The first plywood served as hunting arenas and the second as control.

2.3.2. Primitive Arboreal Ant Species

The colonies, of *P. conradti* were collected from traditional cocoa farms at Ngomedzap (03°16'N, 11°13'E) around the Mbalmayo forest reserve, and Djazeng village (02°31' N, 10°55' E) in the Ntem valley and reared in the laboratory inside a "Chauvin" nest type. The colonies of *P. conradti*, lived inside the plant *Platyserium* epiphytes [8]. Prey foraging by *P. conradti* is most intense between 5:00 and 8:00 AM, while sugary substances are exploited between 5:00 AM and 17:00 PM [8]. Three parallelepiped boxes (each 25×25×5 cm) covered by glass (30×30 cm) were used. The central box serves as nesting box while the two others serve respectively as foraging and control arenas (Figure 1 A & B). Due to their rarity, just five colonies of *P. conradti* were collected from traditional cocoa farms.

2.3.3. Specialized Arboreal Ant Species

During field observations, we noted that *C. clariventris* and *Crematogaster* sp. forage mostly on the trunk while *T. aculeatum* and *O. longinoda* forage on the leaves surfaces. Because of this, a modified protocol of [6] used to study *T. aculeatum* predatory behavior was adopted. The protocol consists for attaching plywood sheets (40 x 51 cm) to tree trunks at one meter above the ground (Figure 1C). For *T. aculeatum* and *O. longinoda*, leave surfaces of the host plant were used as experimental arenas (Figure 1D). The same protocol was applied to study recruitment rate of nestmate in arboreal ants by [14], which justify the presence of control arenas.

2.4. Data Collection

Prey was deposited on the hunting arena. After detection and capture, data collection consists of observing (1) if the prey was cutting or not before transport in the nest; when the cutting occurred (2) we investigated on the fragmentation strategies and transport modalities adopted. Termites and grasshopper of different size were used as prey. For termites, individual workers of 2-3 mm, 5-7 mm and soldiers of 5-8 mm in size were used; for grasshoppers individuals of 4-7 mm, 10-15 mm and ≥ 17 mm were enrolled. To prevent these grasshoppers from jumping, their tibia posterior legs were removed. Thirty interactions were observed for each prey size for a total of 180 observations for each prey type per ant species. No more than three cases were studied for each colony per day.



Figure 1. Experimental apparatus uses to study predatory behavior and fragmentation process of prey in arboreal ants (A) and (B) colony breeding in *Platythyrea conradti*, (C) *Crematogaster* sp. and *Crematogaster clariventris* and (D) for *Oecophylla longinoda* and *Tetramorium aculeatum* [14].

2.5. Data Analysis

We tested the main effect of prey type, morphological caste and prey size on the variation of fragmentation occurrence between ant species using Chi-square tests (GLM Proc). Quantitative data were binary, so we applied binomial errors for the analysis. Analyses were done with R software (version 3.2.2.) and significance was attributed at the 5% level. The data were analyzed with classification tree, using Chi-squared Automatic Interaction Detection (CHAID) method to find the variation in prey fragmentation strategies and transportation modalities between arboreal ant species in relation with prey size and prey type.

CHAID is a type of decision tree technique for nominal scale dependent variable. We considered ant species as an

independent variable; prey size, fragmentation strategies, and number of piece after prey cutting were use as dependent categorical variables. The tree starts with an initial node composed by all the observations and the others correspond for each, to one modality of a considered dependent variable. Chi-square test was used for separation of the best variable. This test helped to separate observations in two groups which lead to the creation of a new node. The same analysis was conducted on the new node and created another node. When the number of observations is not sufficient to create a new node, the analysis stops. The interest of this analysis relies principally on the fact that it permits to organize into a hierarchy dependent variables based on their influence on independent variables in order to show existing interactions between all these variables. The tree classification analysis was run using SPSS 19.0 software and significance was attributed at the 5% level.

3. Results

3.1. Effect of Prey Type and Morphological Caste on Variation of Fragmentation Pattern

In arboreal ant, fragmentation of prey was significantly influenced by prey type ($\chi^2=9.70$; $df=5$; $P<0.0001$), morphological termite caste ($\chi^2=5.93$ $df=5$; $P<0.0001$)

Looking prey type, grasshoppers (45.37%) were more frequently fragmented than termites (20.00%). *Crematogaster clariventris* (88.89%) followed by *Crematogaster* sp. (84.44%) and *T. aculeatum* (67.78%) fragmented grasshoppers more frequently than termites (Table 1). In relation with morphological caste, termite soldiers (45.56%) were more frequently fragmented than workers (13.06%). *Crematogaster* sp. (76.67%), *T. aculeatum* (70.00%), *M. opaciventris* (70.00%) and *C. clariventris* (53.33%) were frequently fragmented termite soldiers than workers (Table 1).

Table 1. Variation of fragmentation occurrence with prey type and termite caste.

Ant species	Prey type		Termite caste					
	Grasshoppers		Termites		Workers		Soldiers	
	A	B	A	B	A	B	A	B
<i>Crematogaster clariventris</i>	10 (11.11)	80 (88.89)	62 (68.89)	28 (31.11)	48(80.00)	12(20.00)	14(46.67)	16(53.33)
<i>Crematogaster</i> sp.	14 (15.56)	76 (84.44)	42 (46.67)	48 (53.33)	35(58.33)	25(41.67)	7(23.33)	23(76.67)
<i>Tetramorium aculeatum</i>	29 (9.83)	61 (67.78)	61 (67.78)	29 (32.22)	58(86.67)	2(13.33)	9(30.00)	21 (70.00)
<i>Oecophylla longinoda</i>	83 (92.22)	7 (7.78)	89 (98.89)	1 (1.11)	60(100.00)	0(0.00)	29(96.67)	1(3.33)
<i>Platythyrea conradti</i>	89 (98.89)	1 (1.11)	90 (100.00)	0 (0.00)	60(100.00)	0(0.00)	30(100.00)	0(0.00)
<i>Myrmecaria opaciventris</i>	70 (77.78)	20 (22.22)	88 (97.78)	2 (2.22)	52(96.67)	8(3.33)	9(30.00)	21(70.00)
Total	295 (54.63)	245 (45.37)	432 (80.00)	108(20.00)	313(86.94)	47(13.06)	98(54.44)	82(45.56)
χ^2 (GLM Proc)	$\chi^2=9.70; df=5$; $P<0.0001$				$\chi^2=5.93$; $df=5$; $P<0.0001$			

A: no prey fragmentation; B: prey fragmentation; for each studied ant species N= 90 respectively for grasshopper and termites, N= 60 for workers and N= 30 for termite soldiers; the value into a bracket represent frequency of occurrence of fragmentation

3.2. Effect of Prey Size on Variation of Fragmentation Pattern

Frequency of fragmentation of termite increased significantly ($\chi^2=11.61$; $df=10$; $P<0.0001$) with termite size. So, in termites, 2.78% of 2-3 mm sized prey were fragmented while 33.89% of 5-8 mm sized prey were fragmented. The highest fragmentation rate was observed in termites of 5-8 mm size for *Crematogaster* sp. (76.67%), *T. aculeatum* (70.00%) and *C. clarientris* (53.33%) (Table 2).

Table 2. Variation of prey fragmentation occurrence with prey sizes in presence of termites.

Ant species	Termites					
	2-3mm		5-7mm		5-8mm	
	A	B	A	B	A	B
<i>Crematogaster clariventris</i>	28(93.33)	2(6.67)	20(66.67)	10(33.33)	14(47.67)	16(53.33)
<i>Crematogaster</i> sp.	28(93.33)	2(6.67)	7(23.33)	23(76.67)	7(23.33)	23(76.67)
<i>Tetramorium aculeatum</i>	30(100.00)	0(0.00)	22(73.33)	8(26.67)	9(30.00)	21(70.00)
<i>Oecophylla longinoda</i>	30(100.00)	0(0.00)	30(100.00)	0(0.00)	29(96.67)	1(3.33)
<i>Platythyrea conradti</i>	30(100.00)	0(0.00)	30(100.00)	0(0.00)	30(100.00)	0(0.00)
<i>Myrmecaria opaciventris</i>	29(96.67)	1(3.33)	29(96.67)	1(3.33)	30(100.00)	0(0.00)
Total	175(97.22)	5(2.78)	138(76.67)	42(23.33)	119(66.11)	61(33.89)
χ^2 (GLM Proc)	$\chi^2 = 11.61$; df= 10; P< 0.0001					

A: no prey fragmentation; B: prey fragmentation; for each studied ant species N= 30 for each prey size respectively; the value into a bracket represent frequency of occurrence of fragmentation

The same trend was observed in grasshoppers where fragmentation occurrence also significantly ($\chi^2 = 2.91$; df= 10; P= 0.003) increased with grasshopper size. Fragmentation occurrence, varied from 36.11% (4-7 mm) to 54.44% (≥ 17

mm). The highest fragmentation rate was observed in *Crematogaster* sp. (96.67%), *C. clariventris* (93.33%) and *T. aculeatum* (80.00%) for grasshoppers greater than 17 mm in size (Table 3).

Table 3. Variation of prey fragmentation occurrence with prey sizes in presence of grasshoppers.

Ant species	Grasshoppers					
	4-7mm		10-15mm		≥ 17 mm	
	A	B	A	B	A	B
<i>Crematogaster clariventris</i>	4(13.33)	26(86.67)	4(13.33)	26(86.67)	2 (6.67)	28(93.33)
<i>Crematogaster</i> sp.	13(43.33)	17(56.67)	0(0.00)	30(100.00)	1(3.33)	29(96.67)
<i>Tetramorium aculeatum</i>	13(43.33)	17(56.67)	10(33.33)	20(66.67)	6(20.00)	24(80.00)
<i>Oecophylla longinoda</i>	28(93.33)	2(6.67)	30(100.00)	0(0.00)	25(83.33)	5(16.67)
<i>Platythyrea conradti</i>	30(100.00)	0(0.00)	30(100.00)	0(0.00)	29(96.67)	1(3.33)
<i>Myrmecaria opaciventris</i>	27(90.0)	3(10.0)	24(80.00)	6(20.00)	19(63.33)	11(36.67)
Total	115(63.89)	65(36.11)	98(54.44)	82(45.56)	82(45.56)	98(54.44)
χ^2 (GLM Proc)	$\chi^2 = 2.91$; df= 10; P= 0.003					

A: no prey fragmentation; B: prey fragmentation; for each studied ant species N= 30 for each prey size respectively; the value into a bracket represent frequency of occurrence of fragmentation

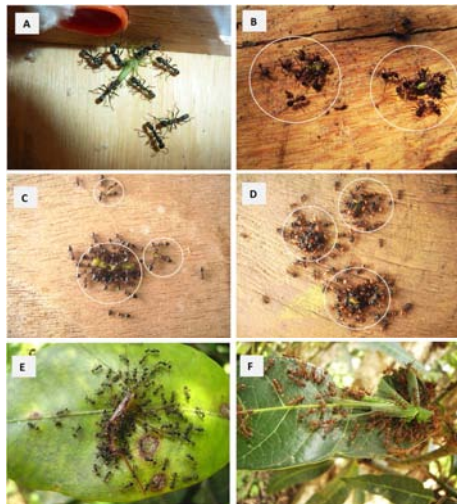


Figure 2. Prey fragmentation and transport modalities in tropical arboreal ant species. A: collective transport by *Platythyrea conradti* workers without prey fragmentation; B: fragmentation in two large pieces by *Myrmecaria opaciventris* worker; each large piece was transported by a group of worker; C: Partial fragmentation, followed by fragmentation in tiny pieces in *Crematogaster* sp.; D: prey fragmentation in three large pieces followed by fragmentation in tiny piece before collective transport in *Crematogaster clariventris*; E: *Tetramorium aculeatum* during spread-eagling before fragmentation in tiny pieces and collective transport and F: partial fragmentation followed by collective transport of the prey by *Oecophylla longinoda* workers.

3.3. Prey Fragmentation and Transport in Arboreal Ant

In arboreal ants, preys were not systematically fragmented after capture; when necessary, they adopt various strategies to fragment their prey before transporting them. The following patterns was observed during prey fragmentation: (1) no fragmentation, frequently observed in *M. opaciventris*, *P. conradti* and *O. longinoda* in presence of small prey size (termite workers of 2-3 mm and 5-7 mm size and grasshopper of 4-7 mm size) where the prey was transported entirely in the nest by a single worker or collective workers (Figure 2A, 2F); (2) total fragmentation found in *T. aculeatum*, *Crematogaster* sp., and *C. clariventris* generally in presence of large prey size (termite soldiers of 5-8 mm size and grasshoppers of 10-15 mm and greater than 17 mm) which involved some individuals totally dismembering their prey into tiny pieces before collective transport by workers (Figure 2E); (3) Partial fragmentation occurred with different sub-modalities including (3.1) appendages broken during spread-eagling found in *O. longinoda* (Figure 2C), in this case appendages and the rest of the prey were transported in the nest without further fragmentation by a worker; (3.2) prey fragmentation in two or three large pieces was noted in *M. opaciventris* (Figure 2B), each large piece was transported by a single worker or collectively by a group of workers; (4)

Partial fragmentation followed by total fragmentation in tiny pieces found in *C. clariventris*, prey was fragmented into two or three large pieces first, after which, each large piece was fragmented into tiny pieces (Figure 2D) before being transported collectively by a group of workers.

3.4. Fragmentation and Transport Modalities in Presence of Termites

In presence of termites, the six ant species did not fragment their prey before transporting them to the nest in 80.0% of cases (Node 0, Figure 3). When fragmentation occurred, different strategies, were adopted, ant species were separated into three nodes significantly distinct ($\chi^2 = 184.406$; $df = 6$; $P < 0.0001$). *Oecophylla longinoda*, *P. conradti* and *M. opaciventris* were grouped in the node 1; these species rarely fragmented termite prey (1.10%) before transportation. *Crematogaster* species and *T. aculeatum* were more likely to fragment prey (Node 2 & Node 3, Figure 3). *Crematogaster*

sp. adopted total and partial fragmentation respectively in 26.70% and 25.60% of observations of termite capture (Node 2, Figure 3). *Crematogaster clariventris* and *T. aculeatum* composed node 3; these species didn't cut termites in 68.30% of the cases; but totally fragmented in 24.4% of the total cases (Node 3, Figure 3). Prey transportation significantly changed depending on the fragmentation strategy adopted in *C. clariventris* and *T. aculeatum* ($\chi^2 = 81.58$; $df = 3$; $P < 0.0001$). When termites were not fragmented by *C. clariventris* and *T. aculeatum*, their transport were done by a single worker or by a collective worker in 100% of the observed cases (Node 4, Figure 3). When fragmentation occurred, *C. clariventris* and *T. aculeatum* transported termites collectively in tiny pieces; sometimes, after partial fragmentation of appendages followed by the transport of the rest of entire prey. But they can also transport prey in a large piece either by a group of workers or by a single worker (Node 5, Figure 3).

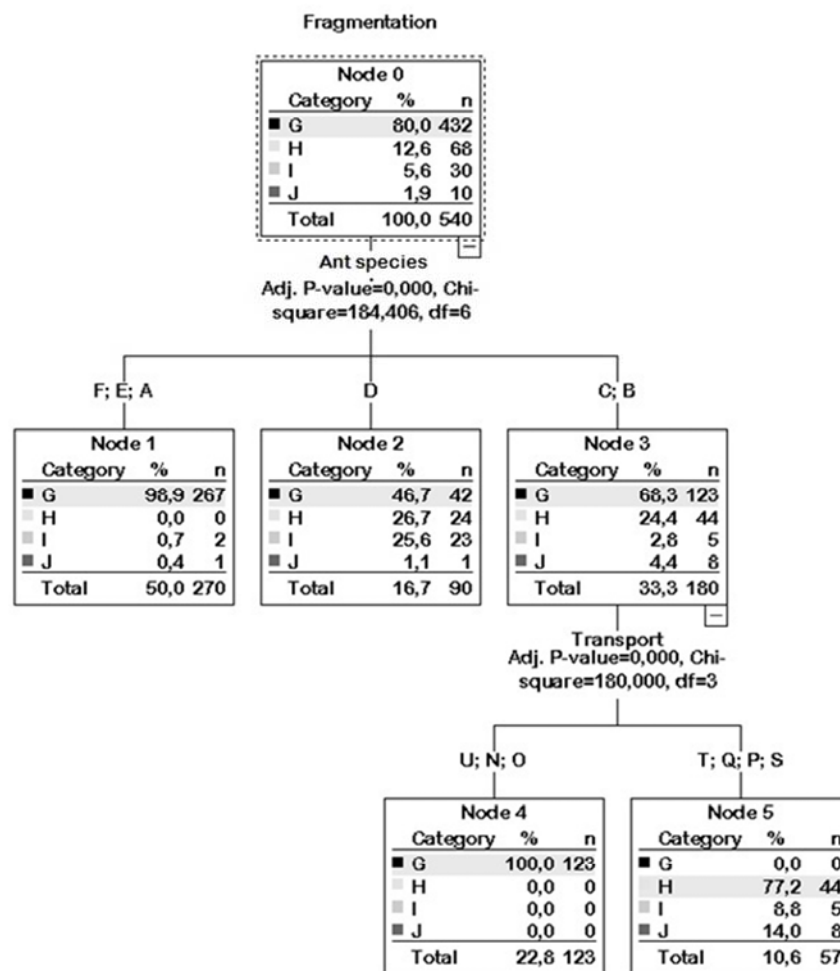


Figure 3. Tree diagram showing hierarchical influence between fragmentation strategy, prey size and transport modalities in six tropical arboreal ants in presence of termites.

3.5. Variation of Number of Pieces During Termite Fragmentation

Almost all termites prey were not fragmented into two or

more large pieces before being transported (Node 0, Figure 4). On the basis of the strategy adopted, ant species were separated in two significantly distinct nodes ($\chi^2 = 9.985$; $df = 1$; $P = 0.049$). Node 1 (Figure 4) contained *Crematogaster* sp.,

O. longinoda, *P. conradti* and *M. opaciventris*. These species fragmented termites (0.60%) into two large piece before transporting them. Node 2 (Figure 4) contained *T. aculeatum* and *C. clariventris*. With the exception of termite soldiers (5-8 mm, 1.7%, Node 3, Figure 4), in this group small prey (2-3

mm) were less frequently fragmented (1.7%, Node 3, Figure 4) than larger prey (5-7 mm) which were more fragmented in large pieces in 10.0% of cases (Node 4, Figure 4) ($\chi^2 = 6.541$; $df = 1$; $P = 0.032$).

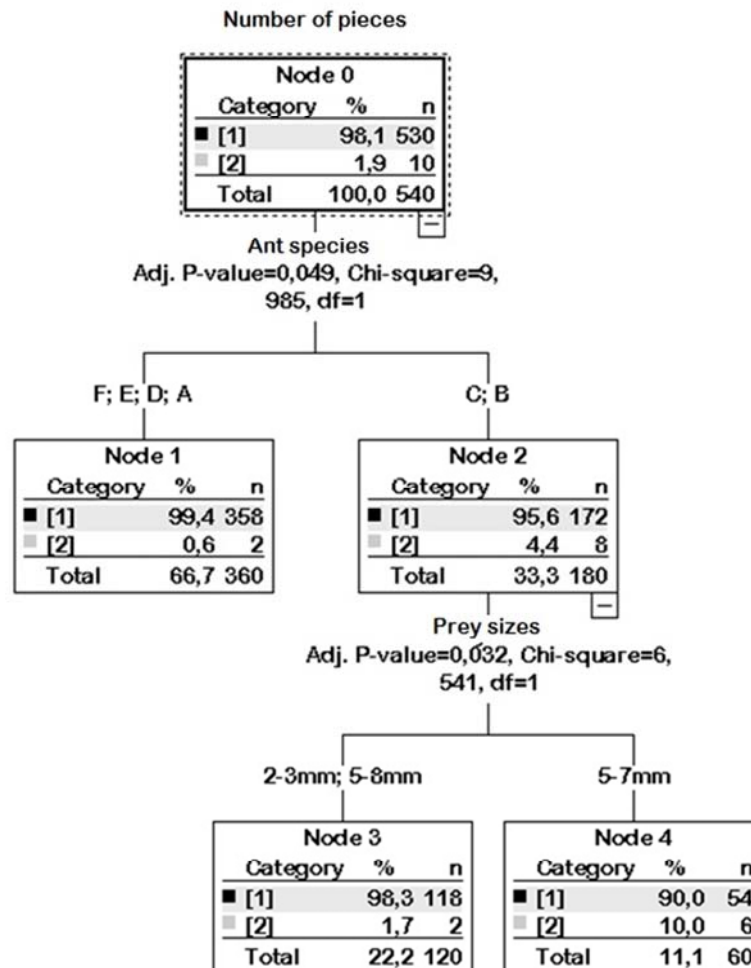


Figure 4. Tree diagram showing hierarchical influence between number of large pieces, ant species and prey size during prey fragmentation in six tropical arboreal ants in presence of termites.

3.6. Fragmentation and Transport Modalities in Presence of Grasshopper

When grasshoppers were the prey item no fragmentation was the most frequent approach observed in the six ant species studied (54.6%) followed by fragmentation in tiny pieces (31.1%) (Node 0, Figure 5). The fragmentation strategies varied significantly between ant species ($\chi^2 = 454.980$; $df = 18$; $P < 0.0001$), and four distinct groups of ant species were observed. The first node is composed of *M. opaciventris* (Node 1, Figure 5) in which no fragmentation was the most frequent strategy (77.80%) followed by fragmentation in two large pieces (18.90%). The second node (Node 2, Figure 5) is composed by *P. conradti* and *O. longinoda*. These species generally did not fragment their prey (95.60%). Nevertheless, in very few case, *O. longinoda* partially fragmented (7.80%) their prey during spread-eagling. Based on this, *O. longinoda* fragmentation strategy

differed significantly from that of *M. opaciventris* ($\chi^2 = 8.209$; $df = 2$; $P = 0.016$) (Figure 5). Node 3 (Figure 5) is composed of *T. aculeatum* and *Crematogaster* sp.. The most frequent fragmentation strategy adopted by these species was fragmentation in tiny pieces. In this group, prey size significantly influenced ($\chi^2 = 84.655$; $df = 3$; $P < 0.0001$) the occurrence of fragmentation pattern. In grasshopper prey 4-7 mm in size the most frequent strategy was no fragmentation (43.3%) while fragmentation in tiny pieces was the most frequent (84.2%) for prey of 10-15 mm and ≥ 17 mm (Nodes 7 & 8, Figure 5). For prey size of 10-15 mm and ≥ 17 mm in *Crematogaster* sp. and *T. aculeatum*, fragmentation in tiny piece was significantly ($\chi^2 = 18.097$; $df = 3$; $P < 0.0001$) more frequent in *Crematogaster* sp. (98.30%) than in *T. aculeatum* (70.00%) (Node 9&10, Figure 5). *Crematogaster clariventris* formed a single group and had diverse prey fragmentation strategies although fragmentation in tiny pieces occurred frequently (63.30%) (Node 4, Figure 5).

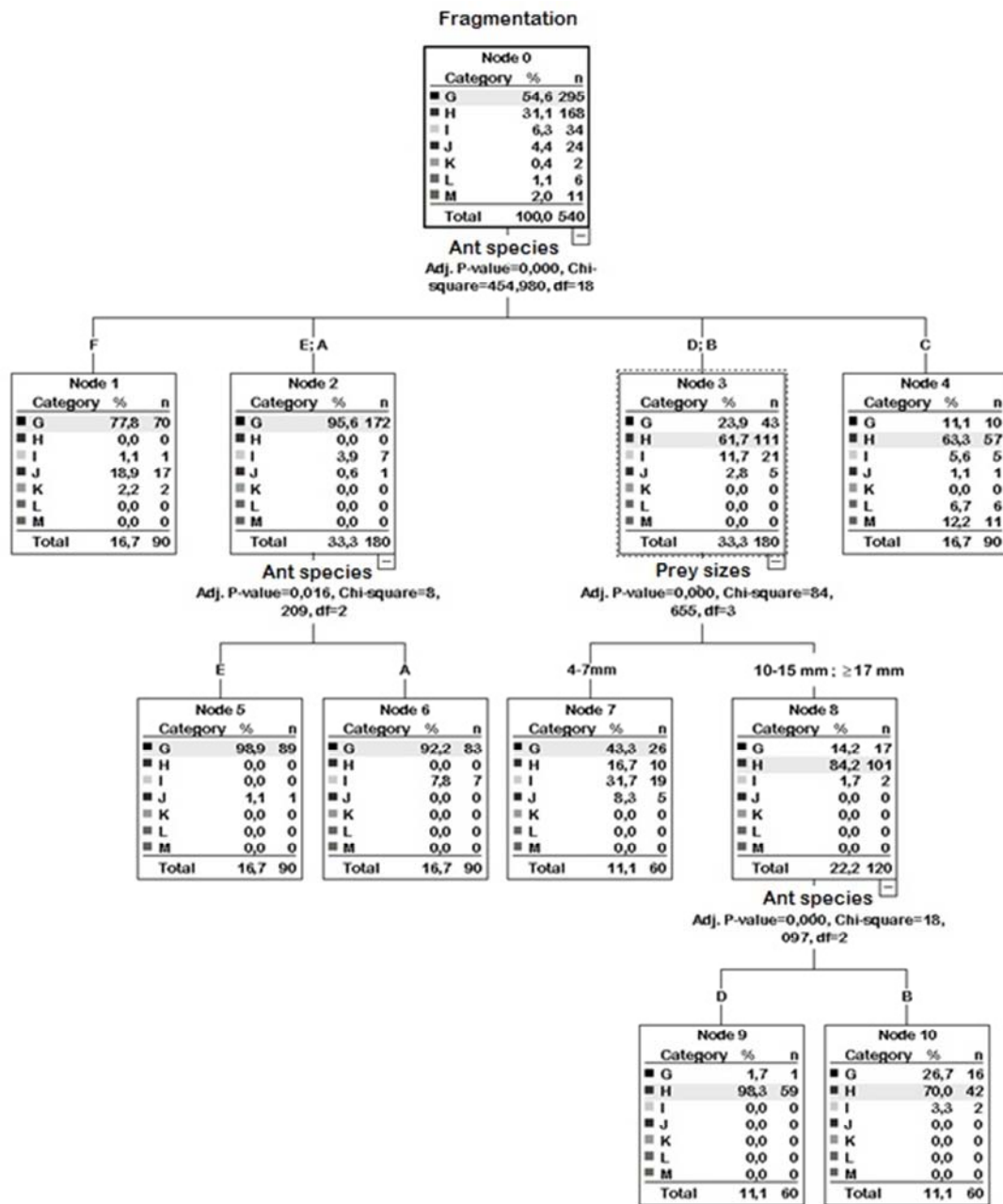


Figure 5. Trees diagrams showing hierarchical influence between fragmentation modalities, prey size and transport modalities in six tropical arboreal ants in presence of grasshoppers.

3.7. Variation of Number of Pieces During Fragmentation of Grasshopper

For grasshopper prey, the primary strategy (92.0%) was to fragment prey in tiny pieces on the spot before transporting them or transport to the nest without fragmentation (Node 0, Figure 6). Fragmentation in two (5.60%) large pieces was more frequent than fragmentation into three (2.4 0%) large pieces before transport. Ant species were grouped into three significantly different nodes ($\chi^2 = 88.750$; $df = 4$; $P < 0,001$). Node 1 contained *M. opaciventris*, node 2 four species including *Crematogaster* sp., *O. longinoda*, *P. conradti* and *T. aculeatum* and node 3 contained *C. clariventris* (Figure 6).

The most common approach in all groups was to exploit the prey without fragmentation. This represented 78.90%, 98.30% and 80.0% of cases respectively for node 1, node 2 and node 3 (Figure 6). *Myrmecaria opaciventris* (Node 1) fragmented grasshopper into two large pieces more frequently than species of node 2 (*O. longinoda*, *T. aculeatum*, *Crematogaster* sp. and *P. conradti*) and node 3 (*C. clariventris*) (Figure 6). Globally, *O. longinoda*, *T. aculeatum*, *Crematogaster* sp. and *P. conradti* shared approximately the same fragmentation strategy with 98.30% of the cases in which the prey was not fragmented into two or three large pieces (Node 2, Figure 6). In the last node, *Cr. clariventris* fragmented their prey more frequently (12.20%)

into three large pieces compared to the other species (Node 3, Figure 6). We also found a significant effect of prey size on the number of large pieces after fragmentation ($\chi^2= 6.864$; $df= 1$; $P= 0,035$) in node 2. In fact, grasshoppers prey size of

4-7 mm (Node 4, Figure 6) were less frequently exploited in one piece (95.8%) than prey size of 10-15 mm and ≥ 17 mm (99.60%) (Node 5, Figure 6).

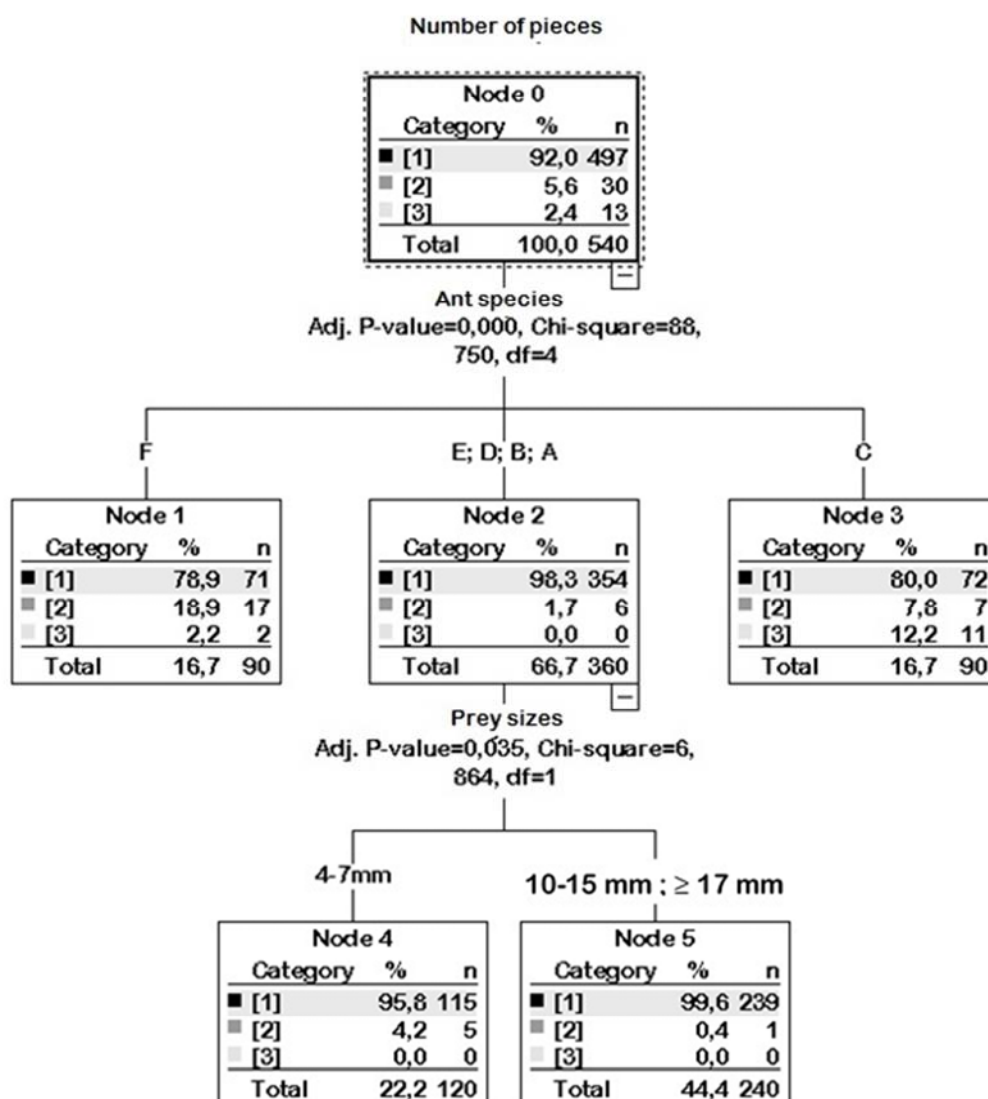


Figure 6. Trees diagrams showing hierarchical influence between number of large pieces, ant species and prey size during prey fragmentation in six tropical arboreal ants in presence of grasshoppers.

Legend of the Figures

Ant species:

A: *Oecophylla longinoda*; B: *Tetramorium aculeatum*; C: *Crematogaster clariventris*, D: *Crematogaster* sp. "stapi", E: *Platythyrea conradti* et F: *Myrmicaria opaciventris*.

Fragmentation modalities:

G: no fragmentation; H: total fragmentation into tiny piece; I: partial fragmentation where workers cut just the appendages; J: partial fragmentation into two large pieces; K: partial fragmentation into three large pieces; L: partial fragmentation into two large piece followed by fragmentation of each large pieces into tiny pieces; M: fragmentation into three large pieces followed by fragmentation of each large pieces in tiny piece.

Transport modalities:

N: solitary transport by a single worker; O: collective transport without prey fragmentation; P: collective transport after prey fragmentation into tiny pieces; Q: collective transport after partial fragmentation of appendages followed by the transport of the rest of entire prey in the nest; R: collective transport after prey fragmentation into two or three large pieces followed by the fragmentation into tiny pieces; S: collective transport of large pieces after partial fragmentation into two or three large pieces, each pieces was transported by a group of workers; T: collective transport of large pieces after partial fragmentation of prey into two or three large pieces, each large piece was transported by a single worker and U: prey escape.

Number of pieces after fragmentation:

[1]: one-piece fragment into tiny pieces or transported entirely by a collective worker in the nest; [2] and [3]: fragmentation into 2 or 3 large pieces respectively.

4. Discussion

Prey fragmentation appears as a fundamental strategy to exploit large prey in ant species. In tropical ant species, small sized prey are not fragmented by species like *M. opaciventris*, *P. conradti* and *O. longinoda* and were generally transported entirely to the nest by either one worker or several workers. [10] described collective transport without fragmentation as cooperative prey retrieval strategy in which several workers cooperate to carry the unfragmented prey. Prey capture and transport without fragmentation has also been described in *O. longinoda* by [9]. In *P. conradti*, unfragmentation is consistent with their solitary hunting behavior [8] and the absence of elaborated nestmates recruitment when a resource is discovered [14]. When the prey size increases, the fragmentation occurred with a variable modality in relation to the level of arboreal adaptation. Collective prey retrieval was observed in *M. opaciventris*, *P. conradti* and *O. longinoda*, total fragmentation in tiny pieces in *T. aculeatum*, partial fragmentation in large pieces in *M. opaciventris* and partial fragmentation in large pieces followed by fragmentation in tiny pieces before transport in the nest was observed in *C. clariventris*. Prey size influenced the number of large pieces obtained after fragmentation; this was observed in the presence of grasshopper where 4-7 mm prey size were more frequently fragmented into two large pieces than 10-15 mm and ≥ 17 mm prey size. In fact, the cuticle of young grasshopper is softer than that of adult; consequently, during spread-eagling it's easier for workers to slice the prey in large pieces before transporting them. During fieldwork we observed that, as prey size increased, workers were helped by the major caste in polymorphic species like *C. clariventris*. During spread-eagling the majors were actively recruited and divided first adult grasshoppers in two or three large pieces, before these were further fragmented into tiny pieces by minor workers and transported. This division of labour appears to be an example of polyethism. We suggest that, this approach may reduce the energy costs invest to prey capture and transport in some arboreal ants. *Tetramorium aculeatum* workers systematically fragmented large prey into tiny pieces before transporting them to the nest. This result is in line with [6] who found high frequency of termites and grasshoppers cutting up in small pieces after spread-eagling in *T. aculeatum* workers. Fragmentation of large prey into tiny pieces by the arboreal ant species such as *T. aculeatum*, *Crematogaster* sp. and *C. clariventris* may facilitate prey transport by workers in compensation of their small size.

We previously observed a relationship between fragmentation strategy, transport modality and nesting habitat. Looking at nesting habitat, it appeared that ground living ant species and primitive arboreal ant are more cooperative in prey retrieval than arboreal ants [10]. We found cooperation in prey retrieval in ground-dwelling ant (*M. opaciventris*), primitive arboreal ant (*P. conradti*) and in some arboreal ants (*O. longinoda*). [10] suggested that prey

fragmentation may be the consequence of prey consumption at capture. This study does not establish relationship between prey fragmentation and prey consumption at capture but suggest that transport modality varies with fragmentation strategy. Two fundamental strategies have been reported including solitary and collective transport [11, 15]. Our result showed that, solitary and collective transport have some specificity depending on fragmentation pattern adopted. For, several studied ant species, single or a group of workers transport unfragmented prey (*M. opaciventris* and *O. longinoda*). When the prey was partially fragmented, each large pieces was transported by a single worker or by a group of worker (*M. opaciventris*). Prey were transported collectively in tiny pieces when total fragmentation occurred (*T. aculeatum*, *C. clariventris* and *Crematogaster* sp.).

5. Conclusion

During prey capture, fragmentation frequency increase with prey type and prey size. In ground-dwelling ants, primitive arboreal ants and in some specialized arboreal ants, collective prey retrieval without fragmentation of small and medium prey sizes was observed. In some specialized arboreal ant, prey was partially fragmented in large pieces follow by total fragmentation in tiny pieces before transport. It seems that, prey fragmentation in tiny pieces was the most achieved strategy observed. Variation in transport modality including solitary transport by a single worker, collective transport of large pieces each by a single worker, collective transport of large pieces each by a collective worker, collective transport of tiny pieces after partial fragmentation followed or not by total fragmentation, was observed. Prey exploitation in *O. longinoda*, considered as high specialized arboreal ant is closer in many aspects to that of the ground-dwelling and primitive arboreal ant.

Acknowledgements

We thank to the Direction board of the “Institut de Recherche Agricole pour le Développement” for the permission to access in Minkoa Mayos orchard for field experimentation. The authors did not receive support from any organization for the submitted work.

References

- [1] Tadu, Z. (2016). Organisation spatiale des communautés de fourmis arboricoles tropicales: rôle structurant et importance du comportement prédateur. Thèse de Doctorat, Université de Yaounde 1, Cameroun.
- [2] Dejean, A., Rodríguez-Pérez, H., Carpenter, J. M., Azémar, F., & Corbara, B. (2017). The predatory behavior of the Neotropical social wasp *Polybia rejecta*. *Behavioral Process* 140: 161–168.
- [3] Lachaud J-P., & Dejean, A. (1994). Predatory behaviour of seed-eating ant: *Brachyponera senaarensis*. *Entomologica Experimentalis et Applicata* 72: 145-155.

- [4] Deneubourg, J. L., Aron, S., Goss, S., & Pasteel, J. M. (1987). Error, communication and learning in ant societies. *European Journal of Operational Research* 30: 168-172.
- [5] Liefke, C., Hölldobler, B., & Maschwitz, U. (2001). Recruitment Behavior in the Ant Genus *Polyrhachis* (Hymenoptera, Formicidae). *Journal of Insect Behavior* 14: 637-657.
- [6] Djiéto-Lordon, C., Richard, F. J., Owona, C., Gibernau, M., Orivel, J., & Dejean, A. (2001b) The Predatory Behavior of the Dominant Arboreal Ant Species *Tetramorium aculeatum* (Hymenoptera: Formicidae). *Sociobiology* 38: 1-11.
- [7] Richard, F. J., Fabre, A., & Dejean, A. (2001). Predatory behaviour in dominant arboreal ant species: the case of *Crematogaster* sp. (Hymenoptera: Formicidae). *Journal of Insect Behavior* 14: 271-282.
- [8] Dejean, A. (2011). Prey Capture Behavior in an Arboreal African Ponerine Ant. *PLoS ONE* 6: 1-7.
- [9] Dejean, A. (1990). Prey capture strategy of the african weaver ant. Westview Press (edit), Boulder, Colorado, USA.
- [10] Yamamoto, A., & Ishihara, S., Ito, F. (2009). Fragmentation or transportation: mode of large-prey retrieval in arboreal and ground nesting ants. *Journal of Insect Behavior* 22: 1-11.
- [11] Kenne, M., Schatz, B., Durand, J. L., & Dejean, A. (2000). Hunting strategy of a generalist ant species proposed as biological control agent against termites. *Entomologica Experimentalis et Applicata* 94: 31-40.
- [12] Tadu, Z., Djiéto-Lordon, C., Yede, Messop-Youbi, E. B., Fomena, A., & Babin, R. (2014). Ant diversity in different cocoa agroforest habitats in the Centre Region of Cameroon. *African Entomology* 22: 388-404.
- [13] Tadu, Z., Babin, R., Yede, Aléné, D. C., Messop-Youbi, E. B., Yede, Wouter, D. & Djiéto-Lordon, C. (2019a). Ant assemblage structure on cocoa trees in smallholder farms in the Centre Region of Cameroon. *African Journal of Ecology*, 00: 1-11.
- [14] Tadu, Z., Bagny Beilhe, L., Aléné, D. C., & Djiéto-Lordon, C. (2019b). Recruitment Rate of Nestmate in Six Tropical Arboreal Ants (Hymenoptera: Formicidae). *Journal of Insect Behavior* (32) 252-266.
- [15] Djiéto-Lordon, C., Orivel, J., & Dejean, A. (2001a). Predatory Behavior of the African Ponerine Ant *Platythyrea modesta* (Hymenoptera: Formicidae). *Sociobiology* 38: 1-13.